

Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes

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Abstract.—The plumage pattern and color and external morphology of hybrid wood warblers (*Dendroica striata* × *Dendroica castanea*) are described. This hybrid combination constitutes the only known case of hybridization between two broadly sympatric species of the genus *Dendroica* (Fringillidae; Tribe Parulini), that is represented by both male and female specimens in definitive alternate plumage. The plumage of the hybrids exhibited a mosaic of character states that varied in the degree of intermediacy between those of the parental species. External measurements of the hybrids fell within the cumulative ranges of characters of the postulated parental species. I hypothesize that the diagnostic predictability of hybrid phenotypes decreases as an inverse function of genetic relatedness of the hybridizing species.

Plumage color patterns are remarkably diverse among the 24 species of *Dendroica* (Aves: Fringillidae; Tribe Parulini) of North America and the Caribbean (taxonomy of Sibley & Monroe 1990), in contrast to the similarity of their body plans and trophic appendages. Several pairs of species thought to have recently diverged (Mengel 1964, Mayr & Short 1970, Bermingham et al. 1992) exhibit striking differences in male definitive plumage, suggesting that plumage pattern may evolve rapidly in response to sexual selection. Our understanding of the inheritance patterns of plumage color in *Dendroica* has been limited to evidence gleaned from hybridization at contact zones between parapatric taxa (e.g., *Dendroica occidentalis* × *Dendroica townsendi*; see Rohwer 1994) and rare instances of intergeneric hybridization (e.g., Parkes 1978, Graves 1993a).

Brodkorb's (1934) description of the hybrid, *Dendroica striata* (Blackpoll Warbler) × *Dendroica castanea* (Bay-breasted Warbler), was the first report of hybridization

between broadly sympatric species of *Dendroica*. This specimen (University of Michigan Museum of Zoology [UMMZ] No. 53692) represents one of the few known intrageneric *Dendroica* hybrids represented by a male in definitive alternate plumage. Because male *D. striata* and *D. castanea* differ dramatically in plumage pattern and color, this specimen assumes unusual significance for the investigation of phenotypic inheritance in avian hybrids.

Recently, the existence of a female hybrid (UMMZ 216628) and an additional male hybrid (San Bernardino County Museum, uncataloged) identified as *D. striata* × *D. castanea*, was brought to my attention, respectively, by Janet Hinshaw and Kenneth Parkes. Here I perform a hybrid diagnosis on all three specimens based on plumage color and pattern and external morphology, following Graves (1990).

Materials and Methods

The male specimen reported by Brod-korb (1934) was collected on 19 May 1920,



Fig. 1. Lateral view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM); and *D. striata* (bottom).

by Norman A. Wood at Warren Dunes, Berrien County, Michigan (Figs. 1–4). The female specimen was collected on 25 May 1970 at Long Point, Ontario, by Joseph G. Strauch (Figs. 5–7). The second male specimen was collected by Lawrence Sansone, III, along the Rio Grande south of Brownsville, Cameron County, Texas, on 9 June 1969. For the purposes of the hybrid diagnosis, I considered all wood warblers that regularly breed north of the Mexican border as potential parental species ($n = 53$).

The first two specimens have broadly tapered rectrices indicating that they were adults in their second year or older (ASY in banding terminology) (Pyle et al. 1987). Plumage, especially the rectrices, of the Texas specimen is moderately worn. Thus, I am uncertain of the bird's age (SY or ASY). Because the specimens appeared to be in definitive plumage, I compared them

to large series of definitive-plumaged specimens in the collections of the National Museum of Natural History, Smithsonian Institution.

For comparative purposes I measured the size of three species: *D. striata*, *D. castanea*, and *D. pinus*. Data for *D. pinus* were omitted from Table 1, after analyses showed that it was not involved in the parentage of the hybrids. Measurements of wing chord, tail length (from point of insertion of central rectrices to tip of longest rectrix), tarsus length, and bill length (from anterior edge of nostril), were made with digital calipers to the nearest 0.1 mm.

I evaluated the color of selected areas of plumage with a Color Mate Colorimeter (Milton Roy), employing a 9.4 mm aperture. The data in Table 2 were compiled from the averages of three independent measurements (specimen removed from ap-



Fig. 2. Dorsal view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM), and *D. striata* (bottom).

erture between trials) per specimen for each plumage area.

Colorimetric characters were described in terms of opponent-color coordinates (L , a , b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be red and green or yellow and blue at the same time. Therefore, "redness" and "greenness" can be expressed as a single value a , which is positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate L , ranging from 0 to 100, describes the "light-

ness" of color; low values are dark, high values are light. In other words, the more light is reflected from the plumage the higher the L value will be.

Difference among character means of presumed parental species were evaluated with two sample t-tests (Wilkinson 1989). Significance of probability values was adjusted for the number of simultaneous tests of morphology (Table 1; $P = 0.05/8 = 0.006$) and plumage color (Table 2; $P = 0.05/12 = 0.004$).

Hybrid diagnoses followed a two-step procedure. First, the presumed parental species of each hybrid were hypothesized through the visual comparison of plumage pattern and color. These hypotheses were then examined with quantitative analyses of

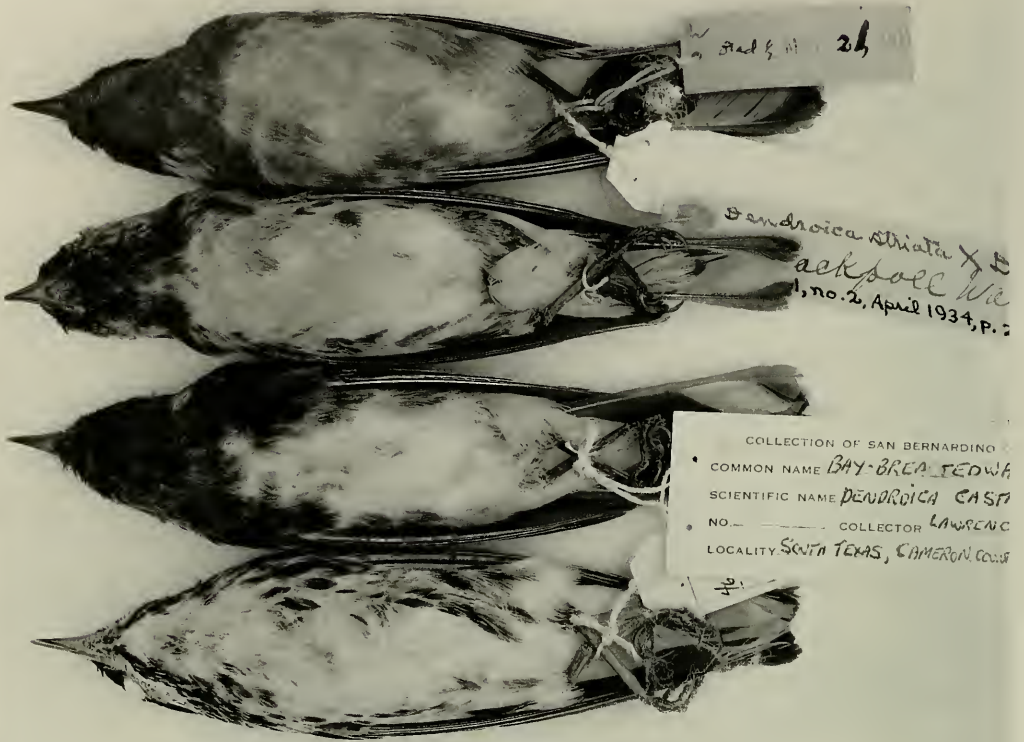


Fig. 3. Ventral view (from top) of males: *Dendroica castanea*; hybrids, *D. striata* × *D. castanea* (UMMZ 53692 and SBCM); and *D. striata* (bottom).

colorimetric and morphometric data. Concordance of results was interpreted as strong support for the presumed parentage of the hybrid (Graves 1990, 1993a; Graves & Zusi 1990).

I used principal components analysis (PCA) on \log_{10} transformed variables to reduce the dimensionality of data and to facilitate the analysis of morphology in two dimensions. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). Because the external measurements of *D. striata* and *D. castanea* overlap (Table 1), both species and sexes were pooled for PCA. Separate PCA for each sex were performed on \log_{10} transformed colorimetric variables of back plumage (Tables 3, 4). Bivariate plots of factor scores from PCA analyses that included both back and crown color were less informative

because significant differences in crown color of the parental species of both sexes polarized the distribution of factor scores.

Results

Plumage Characters

Males.—I concur with Brodtkorb's (1934) identification but his brief, one-paragraph description of the Michigan specimen did not address alternate hypotheses or the external morphology of the parental species (p. 243):

"It is similar to *D. striata*, but differs from the latter species in the following particulars: malar region and chin black, with only the anterior half of the interramal region and a spot one or two millimeters in length at the end of the rami

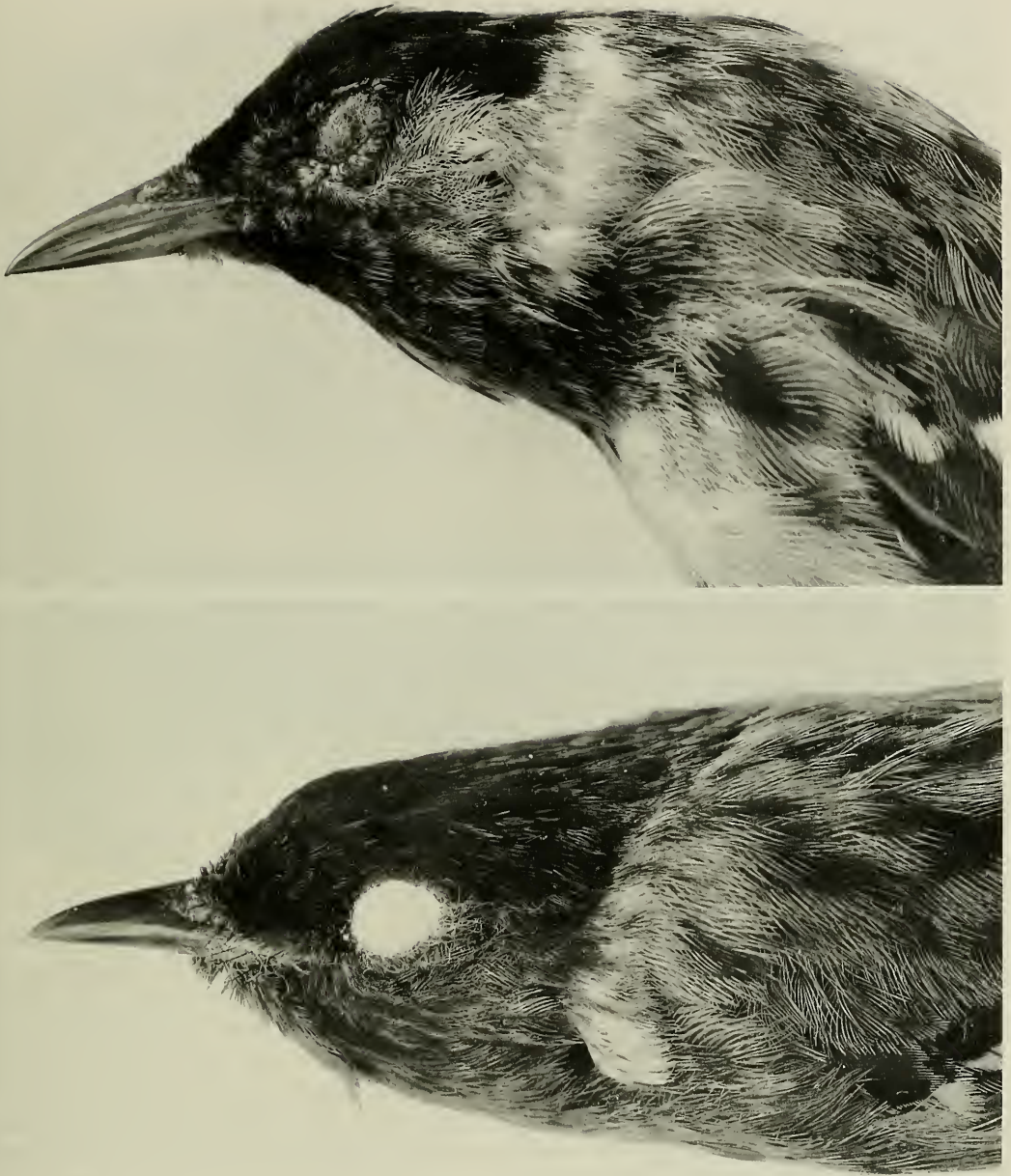


Fig. 4. Lateral view of male hybrids, *Dendroica striata* × *D. castanea*: UMMZ 53692 (top) and SBCM (bottom).

white; black streaks on the sides of throat coalescent, leaving a white line in the center of the throat only one to two mm. broad; chin, malar region, sides of neck, sides and flanks more or less marked with

bay; suborbital, auricular, and postauricular regions, as well as breast, pale cream buff; the abdomen, sides, flanks, and under tail-coverts also somewhat suffused with this color."

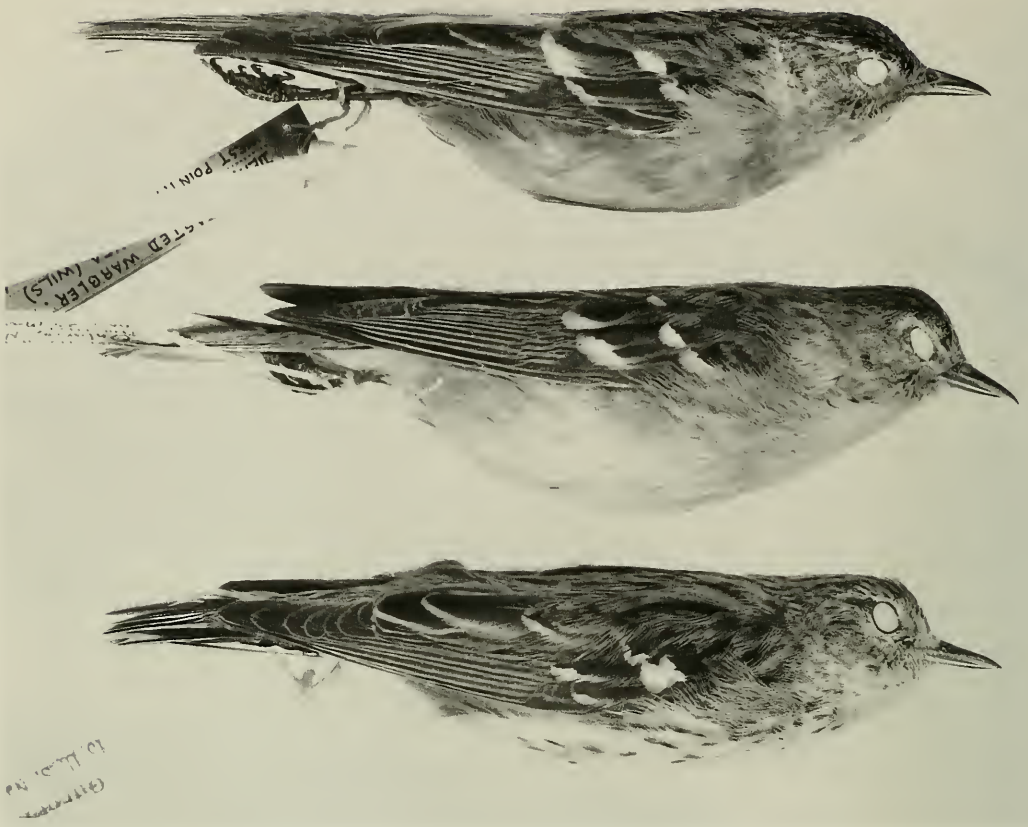


Fig. 5. Lateral view of female *Dendroica castanea* (top), hybrid, *D. striata* × *D. castanea* (UMMZ 216628), and *D. striata* (bottom).

Hybrid wood warblers can be notoriously difficult to identify (Short & Robbins 1967, Graves 1988). In this case, however, identification was expedited by the distinctive characters of the Michigan specimen: (1) black crown (Fig. 1); and (2) mixture of black and chestnut in the malar region (Fig. 2). The black crown of the hybrid, which extends ventrally to the lower margin of the eye, is shared with *Dendroica striata* and the morphologically distinctive *Setophaga ruticilla*. The latter species can be conclusively excluded as a parental species for several reasons, most notably because the rectrices and remiges of the hybrid lack orange or yellow spots, even as traces. Therefore, by default, *D. striata* was one of the parental species. Determination of the other

parental species was also relatively simple. Chestnut and black feathers on upper throat and malar regions of the hybrid could have been contributed only by *Dendroica castanea*.

Although the plumage of the Texas specimen differs in detail from the Michigan male, its diagnostic characters are the same (Appendix 1). In sum, plumage characters of these male hybrids can only be accounted for by two species, *D. striata* and *D. castanea*. Other pairs of warbler species lack the range of pattern elements and plumage colors exhibited by the hybrids.

Female.—Plumage characters of the hybrid that were critical to its identification can be categorized as color or pattern elements, although these are not mutually ex-

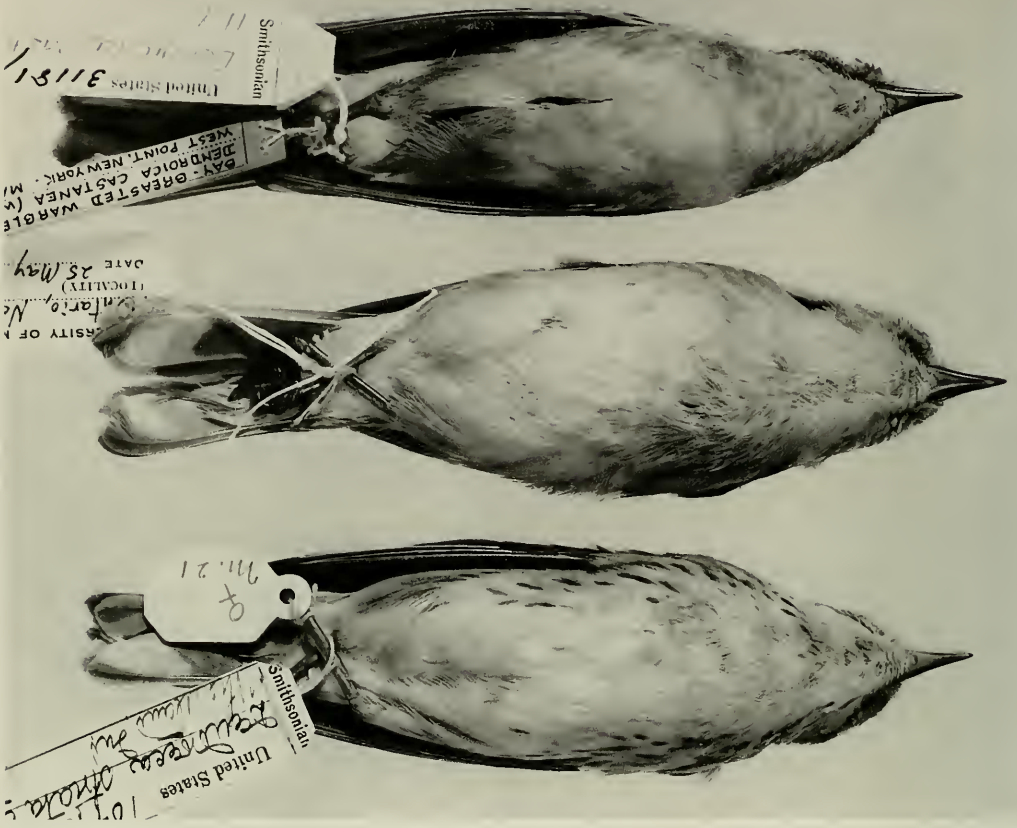


Fig. 7. Ventral view of female *Dendroica castanea* (top), hybrid, *D. striata* × *D. castanea* (UMMZ 216628), and *D. striata* (bottom).

Table 1.—Ranges and means (± one standard deviation) of measurements of definitive-plumaged males and females collected in May and June of *Dendroica castanea*, *D. striata*, and their putative hybrids (University of Michigan Museum of Zoology, No. 53692, ♂; No. 216628, ♀; San Bernardino County Museum (SBCM), ♂). An asterisk indicates that character means of *D. striata* and *D. castanea* differed at $P = 0.006$ ($= 0.05/8$).

Character	<i>striata</i>		<i>castanea</i>		Hybrids		
					UMMZ		SBCM
	♂♂ (n = 12)	♀♀ (n = 12)	♂♂ (n = 12)	♀♀ (n = 12)	♂	♀	♂
Wing chord	71.0 – 76.8	68.6 – 70.7	71.0 – 75.9	68.0 – 72.1	71.3	68.8	70.1
Tail	73.9 ± 1.9	70.7 ± 1.4	73.2 ± 1.5	70.6 ± 1.1			
Tarsus	47.6 – 55.2	47.4 – 50.9	51.0 – 55.6	48.7 – 52.3	50.3	49.5	50.1
Bill	51.3 ± 2.0	*49.8 ± 1.0	52.5 ± 1.4	51.0 ± 1.0			
	18.1 – 19.9	17.5 – 18.7	16.5 – 19.1	16.8 – 18.2	17.5	18.5	18.2
	*18.9 ± 0.6	18.1 ± 0.4	17.8 ± 0.8	17.6 ± 0.5			
	7.7 – 8.8	7.6 – 8.5	7.3 – 8.7	7.4 – 8.4	7.7	7.7	8.3
	8.1 ± 0.3	8.0 ± 0.3	8.1 ± 0.4	7.9 ± 0.3			

Table 2.—Spectrophotometric measurements of back and crown color of male and female *Dendroica striata*, *D. castanea*, and their hybrids. Asterisks indicate character means of *D. striata* and *D. castanea* are significantly different at $P = 0.004$ ($= 0.05/12$).

	Males		Hybrid	
	<i>striata</i> ($n = 12$)	<i>castanea</i> ($n = 12$)	(UMMZ)	(SBCM)
Back				
Lightness (<i>L</i>)	26.5 – 32.9 29.2 ± 2.1	28.8 – 37.0 31.3 ± 2.5	29.4	33.6
Red (<i>a</i>)	0.3 – 1.2 0.8 ± 0.3	0.8 – 3.0 1.4 ± 0.6	1.5	1.4
Yellow (<i>b</i>)	4.7 – 11.1 7.2 ± 1.8	7.1 – 13.1 8.8 ± 1.6	7.9	8.5
Crown				
Lightness (<i>L</i>)	13.0 – 16.9 *14.4 ± 1.4	20.0 – 25.0 22.5 ± 1.6	16.9	14.4
Red (<i>a</i>)	0.2 – 0.9 *0.6 ± 0.2	8.7 – 14.5 12.2 ± 1.8	1.5	2.4
Yellow (<i>b</i>)	0.2 – 2.1 *1.1 ± 0.5	9.5 – 16.6 13.6 ± 2.0	2.4	4.5
Females				
	<i>striata</i> ($n = 12$)	<i>castanea</i> ($n = 12$)	Hybrid (UMMZ)	
Back				
Lightness (<i>L</i>)	28.5 – 33.7 31.6 ± 1.7	29.9 – 34.3 32.6 ± 1.3	33.8	
Red (<i>a</i>)	0.8 – 2.6 1.6 ± 0.6	0.7 – 1.5 1.2 ± 0.2	1.4	
Yellow (<i>b</i>)	9.1 – 14.8 *12.4 ± 1.9	7.5 – 11.6 9.1 ± 1.1	9.0	
Crown				
Lightness (<i>L</i>)	24.5 – 34.1 28.9 ± 3.1	24.3 – 32.4 28.0 ± 2.8	29.8	
Red (<i>a</i>)	0.5 – 2.5 *1.4 ± 0.6	1.0 – 12.9 8.0 ± 3.8	1.4	
Yellow (<i>b</i>)	10.0 – 18.3 13.5 ± 2.3	11.8 – 18.1 14.7 ± 2.0	12.6	

Table 3.—Factor loadings for the first two principal components from an analysis of back color in male *Dendroica striata*, *D. castanea*, and the male hybrids (UMMZ 53692 and SBCM).

Variable	Principal component axes	
	I	II
Lightness (<i>L</i>)	0.007	0.021
Red (<i>a</i>)	0.193	-0.025
Yellow (<i>b</i>)	0.076	0.062
Variance explained	88.4%	10.0%

Table 4.—Factor loadings for the first two principal components from an analysis of back color in female *Dendroica striata*, *D. castanea*, and the female hybrid (UMMZ 216628).

Variable	Principal component axes	
	I	II
Lightness (<i>L</i>)	0.004	0.002
Red (<i>a</i>)	0.137	0.026
Yellow (<i>b</i>)	0.049	-0.073
Percent variance explained	76.4%	21.9%

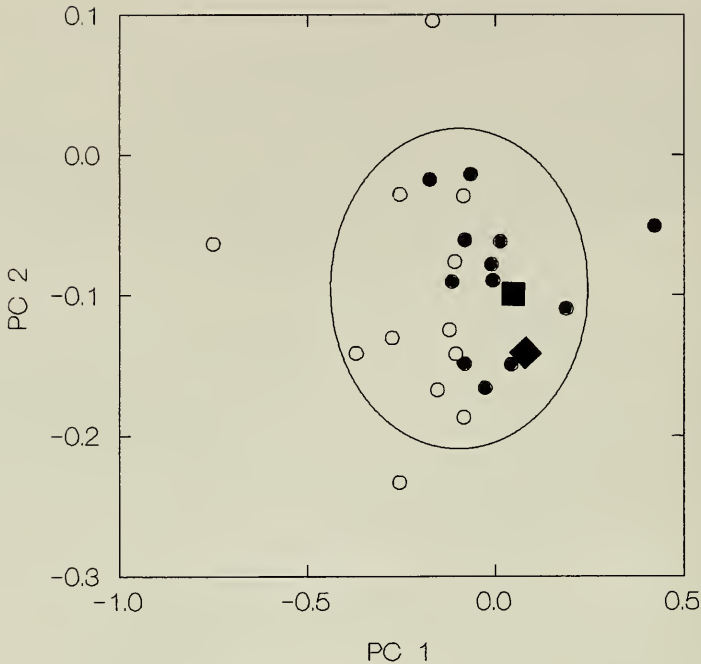


Fig. 8. Bivariate plots of factor scores from a principal components analysis of back color (see Table 3) for male *Dendroica striata* (empty circles), *D. castanea* (filled circles), and *D. striata* \times *D. castanea* hybrids (Michigan hybrid = diamond; Texas hybrid = square). The curved line in this and other plots represents the 95% confidence ellipse.

however, could not have produced the other characters present in the hybrid. Thus, *D. castanea* is clearly indicated as one of the parental species.

The olive crown and muted flank streaks of the hybrid could not have been contributed by *D. castanea* and must be characters of the other parent. Among female wood warblers in definitive alternate plumage, the only species possessing both yellow or olive crowns and lateral ventral streakings are *D. striata* and *D. pinus*. The eye ring, chin, throat, breast, and upper belly of *D. pinus* vary from dull to bright yellow, and its dorsal plumage is heavily saturated with yellow. The hybrid has little yellow in the underparts especially the breast, exhibiting about the same amount of yellow as expressed in series of *D. striata*, but considerably less than that of the dullest, definitive-plumaged *D. pinus*. This suggests that *D. pinus* is highly unlikely to have been a

parental species. Thus, by the process of elimination, the second parental species was *D. striata*.

In sum, the plumage pattern and color of the female hybrid can be accounted for by the two most probable parental species, *Dendroica striata* and *D. castanea* (Appendix 2). Other pairs of species lack the diversity of plumage color and pattern elements exhibited by the hybrid.

Colorimetric Variation

Univariate comparisons.—Male *D. striata* are significantly darker than *D. castanea* on the back and crown, while the back and crown of *D. castanea* are both redder and yellower than those of *D. striata* (Table 2). As Brodkorb (1934) implied in his description, the crown of the Michigan hybrid is similar in general appearance to that of *D. striata* (see Appendix 1). Several of the

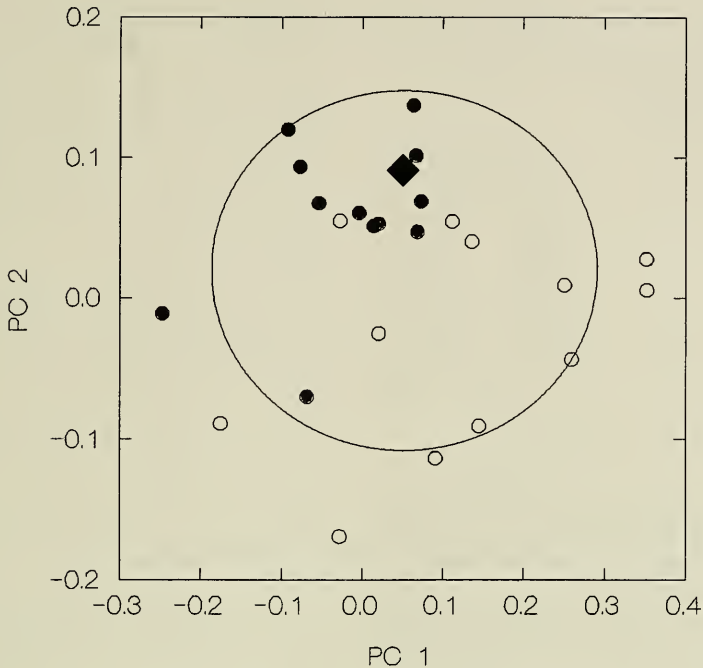


Fig. 9. Bivariate plots of factor scores from a principal components analysis of back color (see Table 4) for female *Dendroica striata* (empty circles), *D. castanea* (filled circles), and a *D. striata* × *D. castanea* hybrid (diamond).

crown feathers of both male hybrids have buffy-olive tips or margins. These cause the colorimetric values for red (*a*) and yellow (*b*) to fall outside the range of values expressed by ASY males of *D. striata*. Back color of the Michigan hybrid is intermediate between that of *D. striata* and *D. castanea*, while values for the Texas hybrid were closer to the characters means of *D. castanea*.

Colorimetric variables of female *D. striata* and *D. castanea* overlap (Table 2). Back color of the female hybrid more closely resembles that of *D. castanea*. The colorimetric values for lightness and redness of the hybrid fall narrowly outside the character ranges for *D. striata*. Crown color variables of *D. striata* and *D. castanea* also overlap, but those of *D. castanea* are significantly redder and slightly yellower. Back color of the hybrid approximates the character means of *D. striata*.

Multivariate comparisons.—Factor scores

from a principal components analysis of back color of male *D. striata* and *D. castanea* overlapped slightly along the first axis, which largely reflected the difference in redness between the species (Fig. 8). The distribution of *D. castanea* along the second PCA axis, which explained only a tenth of the variance, was entirely overlapped by *D. striata*. The male hybrids most closely resembled *D. castanea* in bivariate space and occurred well within the 95% confidence ellipse for hybrids and parental species.

Factor scores for female back color of *D. striata* and *D. castanea* overlapped moderately along the first axis (PCA 1) and extensively along the second (Fig. 9, Table 4). Factor scores in the upper left hand quadrant represent specimens that are redder than average. The female hybrid most closely resembled *D. castanea* in color and fell narrowly outside the zone of overlap of the proposed parental species in bivariate space.

Table 5.—Factor loadings for the first two principal components from an analysis of external measurements of a pooled sample of males and females in definitive alternate plumage of *Dendroica striata*, *D. castanea*, and their hybrids.

Variable	Principal component axes	
	I	II
Wing chord	0.0076	0.0069
Tail	0.0032	0.0123
Tarsus	0.0128	0.0025
Bill	0.0130	-0.0095
Percent variance explained	40.2%	29.6%

External Morphology

As a second step in the diagnosis, hypotheses generated from analyses of plumage characters were tested with analyses of morphological size and shape. Size and shape characters in birds are assumed to be encoded by a multitude of structural and regulatory genes, resulting in additive genetic variation in hybrid morphology. In other words, the external dimensions of hybrids should fall within the cumulative mensural ranges of characters expressed by large samples of the parental species of the appropriate age and sex class.

Univariate comparisons.—External measurements of the male hybrids fell within, or narrowly outside (Texas male) the cumulative ranges of measurements, for male *D. striata* and *D. castanea* (Table 1). Measurements of the wing, tail, and tarsus of the hybrids more closely approached those of the smaller parental species (*D. castanea* in wing and tarsus, *D. striata* in tail). In fact, the wings and tails of male hybrids were more similar in size to females of *D. striata* and *D. castanea* than to males.

External measurements of the female hybrid (Table 1) also fell within the range of measurements of the hypothesized parental species, *D. striata* and *D. castanea*. Wing, tail, and bill measurements of the hybrid were smaller than the character means for females of both parental species, while the hybrid's tarsi were longer than the parental means.

Multivariate comparisons.—Factor scores for male *D. striata* and *D. castanea* overlapped extensively along the first two principal components. In bivariate space, the male hybrids were closely adjacent to individuals of both probable parental species, and well inside the 95% confidence ellipse (Fig. 10a, Table 5).

Females of *D. striata* and *D. castanea* were morphologically less variable than males and primarily occupied the lower left quadrant of the bivariate plot (Fig. 10b). Females of the two species also overlapped less extensively in bivariate space than the respective males. The female hybrid was most similar to *D. striata* in size and shape. Factor scores of the hybrid fell just inside the 95% confidence ellipse surrounding the centroid of female scores.

In conclusion, the univariate and multivariate evaluations of external morphology and plumage color were consistent with the hypotheses generated from the qualitative analyses of plumage pattern and color. This concordance of results provides strong support for the restrictive hypothesis that all three specimens represent hybrids of *Dendroica striata* and *D. castanea*.

Geographic Range.—As neither *Dendroica striata* nor *D. castanea* breed in southern Michigan, southern Ontario, or Texas, the hybrids were presumably migrating when collected. The bulk of the breeding range of *D. striata* is well north of that of *D. castanea*. However, they overlap extensively in the Northwest Territories, British Columbia, Alberta, and Saskatchewan and, to a lesser degree, in the Maritime Provinces of Canada (Godfrey 1986, Erskine 1992). The species are essentially parapatric in northern Manitoba (B. Whitney, pers. comm.) and in central Ontario (Spier 1985), approximately due north of the collection site in Michigan. It is in a region of narrow distributional overlap in Ontario and Quebec, where population densities of *D. striata* and *D. castanea* are low (see Spier 1985), that I expect that hybridization would be most likely to occur. These spe-

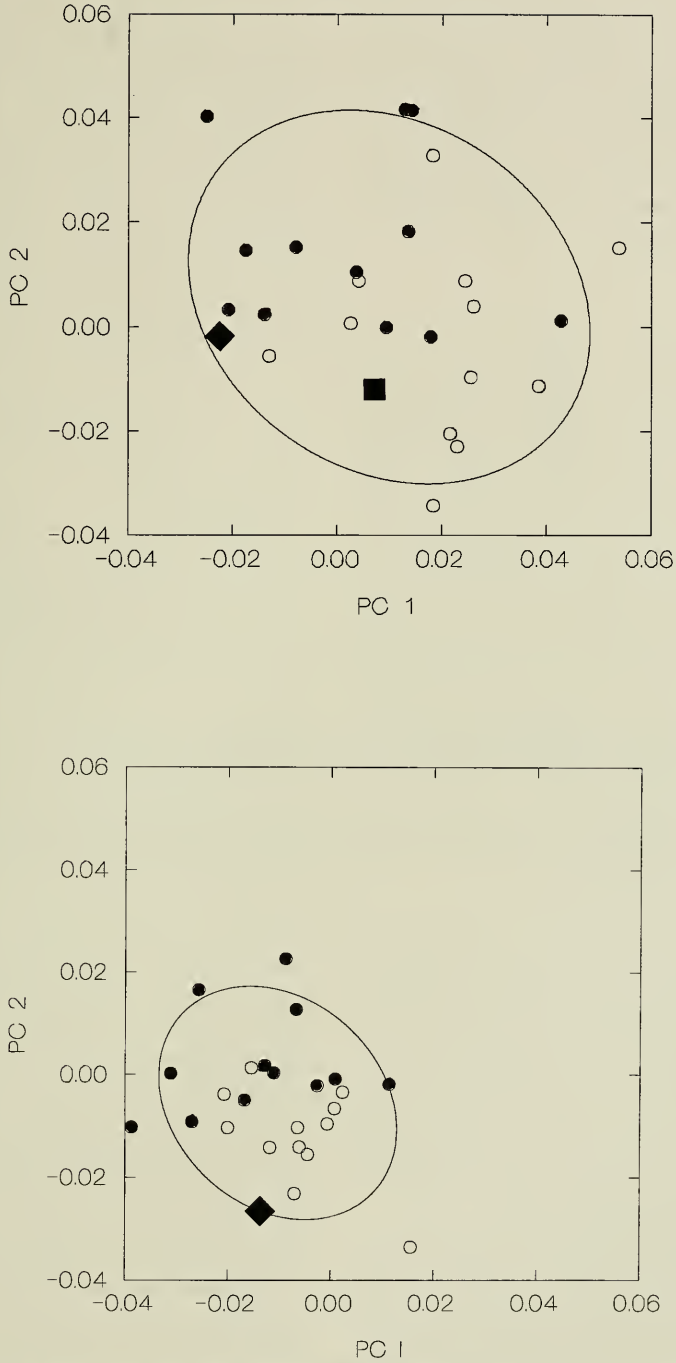


Fig. 10. Bivariate plots of factor scores from a principal components analysis of external morphology (see Table 5) for *Dendroica striata* (empty circles), *D. castanea* (filled circles), and *D. striata* \times *D. castanea* hybrids (Michigan hybrid = diamond; Texas hybrid = square). Factor scores of males (top) and females (bottom) were extracted from the same principal components analysis, but projected on different plots for clarity.

cies in first basic plumage are remarkably similar and some individuals are difficult to distinguish. Juvenile hybrids would be extraordinarily difficult or impossible to detect under field conditions. Thus, surprisingly large numbers of juvenile hybrids could migrate unnoticed to their wintering grounds each autumn.

Conclusions

Hybrid intermediacy in size and shape.—Avian offspring from conspecific matings usually exhibit high heritability of morphological traits (e.g., Boag & Grant 1978, Smith & Zach 1979, Smith & Dhondt 1980, Dhondt 1982). That is, when the values for character traits of the offspring are regressed on the average of those of the parents (for monomorphic species), the slope of the resulting regression line (=heritability) approaches 1.0. These data indicate that the size and shape of passerine birds are largely determined by additive genetic processes, and to a lesser degree, by environmental factors (James 1983). As such, they constitute the empirical foundation upon which the morphological diagnosis of hybrid specimens is permitted.

With a few exceptions (e.g., MacInnes et al. 1989), there have been no comparable studies of morphological heritability in avian hybrids which, strictly speaking, are the result of interbreeding of biological species. Ornithologists have recognized, however, that mensural traits of hybrids were usually intermediate between those of their parental species long before the field of quantitative genetics blossomed (see Falconer 1981).

But what predictions can be made about the morphology of hybrids among distantly related species, especially among those classified in different genera? If the mixture of highly similar genomes results in high heritability, then hybridization between species with dissimilar genetics might be predicted to result in lower heritability. In other words, if heritability, and thus phenotypic predictability, is correlated with the de-

gree of genomic compatibility of the parental species, then the phenotypes of true intergeneric hybrids are relatively unpredictable. Furthermore, the probability that hybrids will deviate significantly from the biparental midpoint may increase as a function of the genetic dissimilarity of the parental species (Fig. 11). In operational terms, there is no reason to expect a hybrid from an intrageneric crossing to occupy a position intermediate to the parental species in multivariate space. As a corollary, it may not be possible to distinguish F_1 , F_2 , or back-crosses among genetically divergent species, if they do occur, on the basis of morphology alone.

Plumage.—Two assumptions, both somewhat vague, are commonly advanced in the analysis of hybrid plumage. The first, that hybrids express plumage characters of both parental species, is bolstered by more than a century of careful study of hybrid specimens (e.g., Cabot 1854), and finds quantitative support in more recent studies that indicate that the pattern and color of most plumage tracts are polygenically controlled (see Hutt 1949, Buckley 1982).

The second assumption is that hybrids do not exhibit plumage characters of species other than their parents (e.g., Banks & Johnson 1961; Graves 1990, 1992, 1993a, 1993b; Graves & Zusi 1990). Rohwer's (1994) use of "contradictory characters" in hybrid evaluation is simply a rephrasing of that hypothesis which, in various guises, also asserts that luxuriance and atavism do not occur in hybrid plumage. As a universal statement, the latter is demonstrably incorrect, because "atavistic" characters occur with frequency in certain anseriform hybrids (Harrison and Harrison 1963). However, atavism has not been adequately documented in other avian orders, and plumage luxuriance has not been documented in any avian hybrid in nature.

In light of the aforementioned assumptions, perhaps my most noteworthy observation on the plumages of the *Dendroica striata* × *D. castanea* hybrids was the ap-

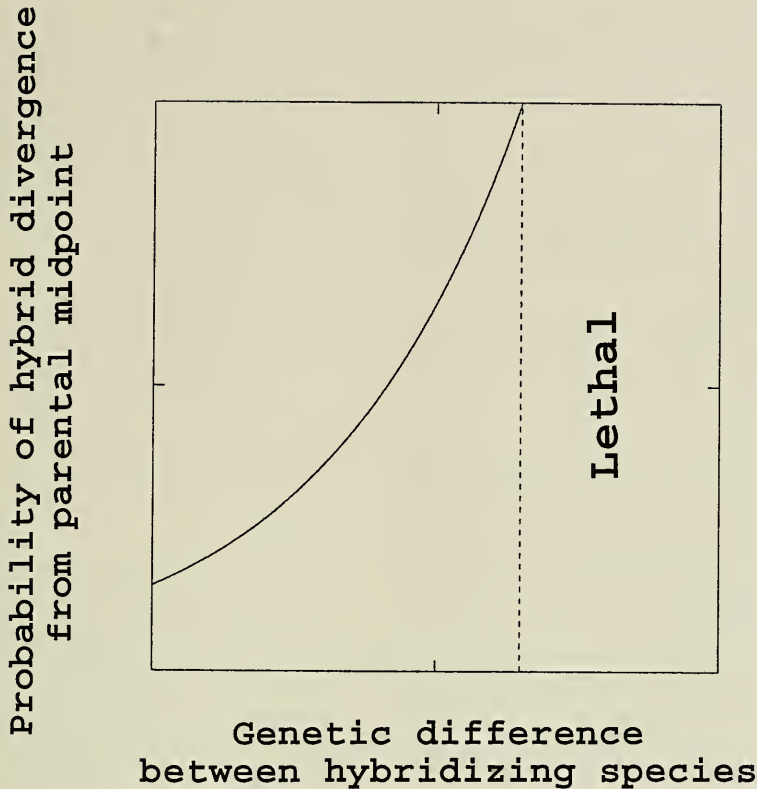


Fig. 11. Hypothetical relationship between the degree of genetic difference between hybridizing avian species and the probability that the morphology of hybrids will significantly diverge from the midpoint of their parental species. The dashed line represents the threshold beyond which hybrids die before hatching.

parent correlation between the degree of difference in colorimetric values of homologous plumage characters of the parental species and the deviation of the hybrid values from the averages of the character means of the parental species (see Table 2). The more discordant the plumage color of the parental species, the more likely that character in the hybrid closely resembled one parental species, rather than a "blended" intermediate (e.g., crown color in males). This pattern can be partially explained by the expansion of possible hybrid values when pigmentation of the parental species differed markedly. It also suggests that a small number of gene complexes control pigmentation of individual plumage tracts in *D. striata* and *D. castanea*. Crown pigmentation of *D. striata* is evidently dom-

inant (or nearly so) to that of *D. castanea* in hybrids, and as Brodkorb (1934) noted, the male hybrid superficially resembles *D. striata* in most respects. Whether this is due to genetic dominance or chance recombination will only be determined with the discovery of additional hybrid males.

Acknowledgments

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Literature Cited

- Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—*Condor* 63:3–28.
- Bermingham, E., S. Rohwer, S. Freeman, & C. Wood. 1992. Vicariance biogeography in the Pleistocene and speciation in North American wood warblers: a test of Mengel's model.—*Proceedings of the National Academy of Sciences USA* 89:6624–6628.
- Boag, P. T., & P. R. Grant. 1978. Heritability of external morphology in Darwin's Finches.—*Nature* 274:793–794.
- Brodkorb, P. 1934. A hybrid in the genus *Dendroica*.—*Auk* 51:243.
- Buckley, P. A. 1982. Avian genetics. Pp. 21–110 in M. Petrak, ed., *Diseases of cage and aviary birds*. 2nd ed. Lea and Febiger, Philadelphia, 680 pp.
- Cabot, S. 1854. Wild hybrid duck, propagated between the *Clangula Americana* (Whistler, or Golden-eye,) and the *Mergus cucullatus*, (Hooded Merganser).—*Proceedings of the Boston Society of Natural History* 5:118–120.
- Dhondt, A. A. 1982. Heritability of blue tit tarsus length from normal and cross-fostered broods.—*Evolution* 36:418–419.
- Erskine, A. J. 1992. Atlas of breeding birds of the Maritime Provinces. Nova Scotia Government, Halifax, 270 pp.
- Falconer, D. S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, London, 340 pp.
- Godfrey, W. E. 1986. The birds of Canada, revised edition. National Museum of Canada, Ottawa, 595 pp.
- Graves, G. R. 1988. Evaluation of *Vermivora* × *Oporornis* hybrid wood warblers.—*Wilson Bulletin* 100:285–289.
- . 1990. Systematics of the “green-throated sunangels” (Aves: Trochilidae): valid taxa or hybrids?—*Proceedings of the Biological Society of Washington* 103:6–25.
- . 1992. Diagnosis of a hybrid antbird (*Phlegopsis nigromaculata* × *Phlegopsis erythroptera*) and the rarity of hybridization among subspecies.—*Proceedings of the Biological Society of Washington* 105:834–840.
- . 1993a. A new intergeneric wood warbler hybrid (*Parula americana* × *Dendroica coronata*) (Aves: Fringillidae).—*Proceedings of the Biological Society of Washington* 106:402–409.
- . 1993b. A new hybrid manakin (*Dixiphia pipra* × *Pipra filicauda*) (Aves: Pipridae) from the Andean foothills of eastern Ecuador.—*Proceedings of the Biological Society of Washington* 106:436–441.
- , & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Helianthus amethysticollis*) from northern Colombia.—*Condor* 92:754–760.
- Harrison, J. M., & J. G. Harrison. 1963. Comments on a hybrid Red Shoveler × Northern Shoveler.—*Bulletin of the British Ornithological Club* 83:21–25.
- Hunter, R. S., & R. W. Harold. 1987. The measurement of appearance. 2nd edition. Wiley, New York, 411 pp.
- Hutt, F. B. 1949. Genetics of the fowl. McGraw-Hill, New York, 590 pp.
- James, F. C. 1983. Environmental component of morphological differences in birds.—*Science* 221:184–186.
- MacInnes, C. D., R. K. Misra, & J. P. Pevett. 1989. Differences in growth parameters of Ross' Geese and Snow Geese: evidence from hybrids.—*Canadian Journal of Zoology* 67:286–290.
- Mayr, E., and L. L. Short. 1970. Species taxa of North American birds. Publication No. 9 of the Nuttall Ornithological Club, Cambridge, Massachusetts.
- Mengel, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae).—*Living Bird* 3:9–43.
- Parkes, K. C. 1978. Still another parulid intergeneric hybrid (*Mniotilta* × *Dendroica*) and its taxonomic and evolutionary implications.—*Auk* 95:682–690.
- Pyle, P., S. N. G. Howell, R. P. Yunick, & D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California, 278 pp.
- Rohwer, S. 1994. Two new hybrid *Dendroica* warblers and new methodology for inferring parental species.—*Auk* 111:441–449.
- Short, L. L., Jr., & C. S. Robbins. 1967. An intergeneric hybrid wood warbler (*Seiurus* × *Dendroica*).—*Auk* 84:534–543.
- Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.
- Smith, J. N. M., & A. A. Dhondt. 1980. Experimental confirmation of heritable morphological variation in a natural population of song sparrows.—*Evolution* 34:1155–1160.
- , & R. Zach. 1979. Heritability of some morphological characters in a song sparrow population.—*Evolution* 33:460–467.
- Speirs, J. M. 1985. Birds of Ontario. Volume 2. Natural Heritage/Natural History Inc., Toronto, 986 pp.
- Wilkinson, L. 1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.

Appendix 1

Comparative descriptions of the male hybrids, *Dendroica striata* × *Dendroica castanea*, and their parental species in definitive alternate plumage (Figs. 1–4). Hybrids are referred to as the “Texas” (SBCM) and “Michigan” (UMMZ 53692) specimens, respectively.

The crown, superciliary, and lores are semi-glossy black in *striata* (Fig. 1). In *castanea*, the forecrown is black becoming into chestnut on the crown above the eyes, and extending posteriorly to the rear crown; the superciliary and lores are black. The respective parts of the Michigan hybrid resemble those of *striata*; a few feathers above the nostrils and on the superciliary have faintly buffy-olive tips; several feathers of the hind-crown have broader buffy-olive margins. The crown of the Texas specimen is more intermediate in appearance. Feathers of the hindcrown are margined with buff-olive, imparting a streaked appearance. Several small chestnut spots occur on feathers of the mid-crown.

The parental species and the hybrids have a thin nuchal collar: black streaked with white in *striata*, buffy-white in *castanea*, pale buffy-white in the Michigan hybrid, and dull olive-buffy in the Texas hybrid. Feathers on the mantle, scapulars, lower back, rump and uppertail coverts of *striata* have black center stripes and broad gray margins. The respective plumage of *castanea* is similarly patterned but the feather margins are buffy-olive on the mantle, changing to gray on the lower back, rump, and undertail coverts. In the hybrids, dorsal plumage posterior to the hindcrown is nearly intermediate in appearance to that of the parental species.

D. striata has a white facial patch that extends from the base of the lower mandible, posteriorly to the ventral eyering and the auriculars. The respective parts of *castanea* are black. In *striata*, the white facial patch of *striata* is bordered ventrally by a thin black malar stripe, which originates on the chin and extends to the upper breast, and posteriorly by vertical zebra-like striping on the nuchal collar. The black “face” of *castanea* is bordered ventrally by the chestnut throat, and posteriorly by a large buff neck patch, a ventral extension of the nuchal collar. The facial plumage of the Michigan hybrid expresses a complex mosaic of the parental characters (Fig. 4). Feathers adjacent to the bill are black with pale buffy-white tips; while those on the lower eyering and auriculars are grizzled dark gray and buffy-white. The auriculars are bordered posteriorly by a buffy-white neck patch, which is paler and smaller than that of *castanea*. Facial plumage of the Texas hybrid is considerably darker than that of the Michigan hybrid, and similar in appearance to *castanea*. The posterior auriculars are grizzled (sooty black and gray), and bordered posteriorly by a dull, silvery-buff, neck patch, which is smaller and less distinct than in *castanea*.

The remiges and wing coverts of *striata* and *cas-*

tanea are similarly patterned; the greater and middle wing coverts are tipped with white in *striata* but are more broadly tipped with pale buffy-white in *castanea*. The hybrids’ wings are intermediate in pattern and color. White spots in the outer rectrices of the hybrids are intermediate in size and shape between those of *striata* and *castanea*.

The throat, breast, belly, and undertail coverts of *striata* are white bordered laterally by black streaking on the sides of the throat, breast, and flanks. The chin of *castanea* is black, bordered posteriorly by chestnut, which extends posteriorly to the upper breast along the midline and laterally to the flanks; the center of the breast, lower belly, and undertail coverts are buffy-white. The feathers of the Michigan hybrid’s throat are grizzled with black and chestnut, many faintly tipped with white, especially on the chin and along the midline, imparting the appearance of wide malar stripes. The breast, belly, and undertail coverts of the Michigan hybrid are white, faintly tinted with buff; the flanks are marked with muted brownish-black spots and streaks and a strong chestnut wash. The chin, throat, upper breast, and sides of the Texas hybrid are “roan” (sooty black, subtly grizzled with chestnut and pale gray) in a pattern mirroring the distribution of chestnut in *castanea*. Center of the breast, belly and undertail coverts of the Texas specimen are pale buffy white. A few indistinct pale chestnut and sooty spots are found on the flanks.

Appendix 2

Comparative descriptions of the female hybrid (UMMZ 216628), *Dendroica striata* × *Dendroica castanea*, and its parental species in definitive plumage (Figs. 5–7).

Feathers of the crown, scapulars, and mantle of *striata* are olive to grayish-olive with pronounced blackish-brown shaft streaks. The respective plumage of *castanea* is olive-gray to gray but more heavily streaked with black; feathers of the crown, from the eyes to the nape, are chestnut distally with grayish-olive margins. The crown of the hybrid is more heavily streaked than in *striata*, but less so than in *castanea*; feather margins are olive (a few grayish-olive) and exhibit no trace of chestnut pigmentation on the basal or distal barbs under magnification (7×). The mantle of the hybrid, which contrasts with its olive crown, is intermediate in appearance between those of the parental species. The rump and uppertail coverts are olive-gray in *striata* and gray in *castanea*. The hybrid has an olive-gray rump and gray uppertail coverts.

The short superciliary of *striata* is poorly defined by pale olive to pale yellow feather tips. In *castanea* the superciliary is even more poorly defined and streaked with dark gray and black. The lores and auriculars of *striata* are mottled olive-gray, bordered posteriorly by a faintly perceptible olive-gray patch on the side of the neck. The lores and auriculars of *castanea* are more heavily pigmented and contrast with the throat and a

well-defined buff neck patch. Pigmentation of the superciliary, lores, and auriculars of the hybrid falls within the range of variation found in *striata*, but the auriculars are bordered posteriorly by well-defined buffy neck patch as in *castanea*.

White tips of the middle and greater wing coverts of the hybrid are intermediate in width between those of *striata* and *castanea*. Outer margins of the rectrices are olive-gray in *striata* and the hybrid and gray in *castanea*.

The venter of *striata* is white tinted with pale yellow

or olive on the throat and breast; narrow black streaking occurs on the side of the throat, breast, and flanks. The venter of *castanea* is buffy-white to buff, extensively suffused with chestnut on the throat, side of the breast, and flanks. The throat, upper breast, and flanks of the hybrid are buff, fading to pale buffy-white on the belly and undertail coverts. Several flank feathers are marked with pale chestnut and faint muted streaks appear at the side of the breast. The dried tarsi of the hybrid are intermediate in color between those of *striata* (light brown) and *castanea* (dark brown).